

TAXONOMIC PROBLEMS IN THE STUDY OF COCCOLITHS

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ABSTRACT. From a review of Jurassic, Cretaceous, Tertiary, and Recent coccolithophorid and discoaster material, it is suggested that the abrupt appearance of some complex forms, hitherto difficult to classify, may be explained by mineralization of already existing unmineralized stocks; it also seems likely that some living un-mineralized forms may have fossil mineralized ancestors. Some recent work on uncalcified Haptophyceae reveals interesting parallels with the coccolithophorids. One new family, Stephanolithaceae, is erected, and four specific names are recorded in new combination.

LIVING in the present oceans there are about 200 species of coccolith-bearing algae. About half of these fall quite naturally into two big families; the rest make up a peculiarly heterogeneous collection, with numerous monospecific genera which are very difficult to group into families or higher taxa. Attempts to devise a scheme of classification for these organisms have not been entirely successful. The simpler schemes tend to force very diverse genera into an inappropriately small number of families, as may be seen in many reports on quantitative plankton-surveys. Some of the more elaborate schemes try to solve the problem by building up a theoretical phylogenetic tree which is used as a basis of classification. For this purpose, the evidence has been drawn exclusively from the comparative morphology of living species, and up to the present palaeontological observations have been almost completely ignored. Twenty years ago, this may have been excusable, but it is not so today, for there is now enough information at hand for us to start establishing phylogenetic series on the evidence of the fossil record.

When we attempt to do this, one of the first results is the discovery that the two largest families, the Syracosphaeraceae and Zygosphaeraceae, each with more than 50 living species, have virtually no geological record at all. With the smaller taxa, the situation is quite different; many of the systematically isolated genera are found to have long ancestries, and some are survivors from once prosperous Mesozoic or Tertiary families. Clearly, these survivors are more closely related to their own fossil ancestors than they are to living genera of different parentage, and it is no longer reasonable to lump all the living coccolith-bearing algae into a single family, as has been done in some of the most recently published classifications (Kamptner 1958, pp. 68-71, Deflandre 1966, pp. 5-6).

Considerations such as these suggest that the time has now arrived when we must look carefully at the impact of palaeontological research upon the taxonomy of living forms. During the last two decades there has been a strong tendency to deny the possibility of recognizing fossil representatives of many living taxa above the rank of species. This is, of course, a strictly logical attitude, because the micropalaeontologist has to work largely with individual coccoliths, and some modern genera are defined in terms that take into account the way in which the coccoliths are assembled to form a complete skeleton. Nevertheless, I think it is an unnecessarily defeatist attitude, because it assumes that each fossil coccolith is to be considered as a completely isolated entity, with no

ancestors and no descendents. This, of course, is not true, and I hope to show that many living taxa can be traced back with reasonable confidence into the Tertiary, and a few can be followed still further into the Mesozoic. In this way, family relationships sort themselves out as phylogenetic lineages, and the theoretical difficulties of working with isolated coccoliths fall into the background.

PROBLEMS IN THE CLASSIFICATION OF LIVING COCCOLITHOPHORES

From the early days, it has been found satisfactory to identify and classify the living species on the basis of coccolith-structure. No two species are known which have exactly similar coccoliths, and, as a working hypothesis, it is not unreasonable to assume that this also holds good for extinct species. Coccolith-structure has likewise been relied upon extensively for the delimitation of genera, but other characters such as the shape of the cell and the presence or absence of a naked area at the flagellar pole have also been used to some extent in defining genera and higher taxa. Living taxa defined purely in terms of coccolith-morphology can be recognized with certainty when they are found as fossils, but characters involving the arrangement of coccoliths on the cell-surface are not as a rule observable in fossil material. With this difficulty in mind, some micropalaeontologists have argued that all fossil coccoliths should be assigned to provisional taxa until a complete coccosphere has been discovered. This practice has the serious disadvantage of requiring a dual nomenclature, with one set of names for living material and another for fossils, thus creating an artificial break between modern forms and their fossil ancestors.

In order to resolve this problem, we will first of all look more closely at some of the taxonomic difficulties presented by living coccolithophores, and then try to discover just how serious these difficulties really are when we try to work out some sort of phylogenetic story.

Dimorphism of coccoliths

Lohmann (1902) found that in some species the coccoliths covering a single individual were not all alike; for example, those round the flagellar pole might bear spines, whereas the ordinary body-coccolith did not. Usually the polar coccoliths are easily recognizable as straightforward modifications of the normal type, and Lohmann did not in general segregate species with this kind of dimorphism into separate genera. The only genus which he distinguished on these grounds was *Scyphosphaera*, which has an equatorial girdle of very large float-coccoliths. Taxonomic difficulties did not arise until 40 or 50 years later, when Kamptner (1941) and Deflandre (1952) took a much more serious view of coccolith-dimorphism, and removed all species with dimorphic coccoliths into separate genera. The consequent practical difficulty in naming fossil coccoliths was perhaps unnecessarily exaggerated, but the theoretical implications led Deflandre to abandon the use of a single classification for both living and fossil forms, and to create an independent taxonomic system for the fossils. The general adoption of this policy during the decade that followed did much to retard progress in the study of phylogenetic and taxonomic relationships among the fossil coccoliths.

Coccolith-dimorphism is likely to have been prevalent to much the same extent in

fossil as in living taxa, and although final proof is usually beyond our reach, it is not difficult to find fossil examples of morphological variants that have all the earmarks of dimorphic pairs. These are not uncommon in *Cretarhabdus* (Pl. 150, figs. 4, 5), *Deflandrius* (Pl. 151, figs. 4, 5), *Kamptnerius* (Pl. 152, figs. 5, 6), and *Rhabdolithina*; if fossil species with dimorphic coccoliths are not recognized as such, the worst that can happen is that two species with identical ranges appear in the fossil record instead of one.

Pleomorphic life-histories

Observations on the life-histories of species kept in culture have brought to light several examples in which a motile coccolith-bearing phase alternates with a sessile uncalcified phase which had previously been accepted as a member of a different genus (Parke 1961). This is particularly true of coastal species, whose non-motile phases tend to live attached to rocks. Distinct from these are the pelagic species, whose resting-stages take the form of calcified cysts, which in the absence of any solid support, remain suspended in sea-water. One of these species, *Crystallolithus hyalinus*, which bears organic scales, sometimes unmineralized (Pl. 154, figs. 1, 2), and sometimes covered with minute rhombohedra of calcite, has proved to be the motile phase of *Coccolithus pelagicus*, an encysted form with coccoliths of a totally different kind (Pl. 143, figs. 1, 2).

These unexpectedly complicated life-histories are interesting from a taxonomic point of view, because the individual phases are usually so different from each other that they were put into separate genera when first discovered. To judge from our knowledge of living species, we can hardly expect to find tangible evidence of pleomorphism in the fossil record. In the coastal species, all the known sessile phases are uncalcified, and hence unlikely to be preserved as fossils. In the pelagic species, on the other hand, it is only the heavily calcified cysts, or their component coccoliths, that stand much chance of being preserved; delicate motile forms like *Crystallolithus* soon disintegrate, and are never found in bottom deposits. Indeed, material from living cultures needs careful handling in the laboratory to prevent the organic scales from losing their cover of calcite crystals. The cysts, on the other hand, are often preserved entire, and good examples are quite common in rocks as old as the Kimeridge Clay (Pl. 143, fig. 6).

Variation in response to external conditions

Changes in external conditions can, in some circumstances, cause the organism to modify the appearance of its coccoliths, or even to cease calcification.

In most species that have been experimented upon, the principal effect of temperature-change is to alter the rate of cell-multiplication, without any significant effect upon coccolith-morphology. In *Coccolithus huxleyi*, however, the coccoliths grown in warm water are reported to be distinguishable from those grown at low temperatures (Pl. 145, figs. 1, 2); the two variants have been recorded in laboratory cultures (Watabe and Wilbur 1966) and in natural populations (McIntyre and Bé 1967).

C. huxleyi is kept in culture in several laboratories, and a number of separate strains are kept under constant observation. Some of these have been found quite suddenly to stop growing coccoliths, and to persist in a naked condition (Paasche 1964, p. 11). One cause of this change appears to be an enrichment in the supply of nutrients, particularly phosphate. An interesting point is that whereas some strains will resume growth

of coccoliths if the culture medium is adjusted to a composition more like natural seawater, others will not, and no known treatment will induce them to do so.

There are several very suggestive possibilities here in connection with the evolution and taxonomy of these algae; fixation of a single phase out of a pleomorphic life-history, independent development of ecological variants, and sudden changes from a naked to a calcified condition, could all lead to the introduction of apparently cryptogenetic forms into the geological record. Furthermore, some of these changes could take place very suddenly, owing to the extraordinarily fast rate of multiplication that is prevalent in these organisms (Parke and Manton 1962).

PHYLOGENETIC HISTORY OF SOME LIVING TAXA

Attempts to trace living coccolithophorids back into geological history lead to curiously divergent results. Some species such as *Coccolithus pelagicus*, *C. huxleyi*, and *Braarudosphaera bigelowi* lead back to flourishing and diverse complexes, which in the present oceans have been reduced to just one or two surviving representatives. The ancestral stocks show a good deal of evolutionary divergence, but a set of unifying family characters persists throughout. *Pontosphaera* provides an extreme example of divergence, for we not only get a hint of an evolutionary connection with the extinct Zygothaceae, but we also find here the first suggestion of a far-distant linkage with another living family, the Helicosphaeraceae. Other stocks seem to have been peculiarly stable throughout their geological history. *Calciosolenia* can be traced back to mid-Cretaceous times with very little change, and the coccoliths of *Braarudosphaera bigelowi* are specifically indistinguishable from fossils preserved in early Cretaceous rocks. In contrast with these are two flourishing modern families, the Syracosphaeraceae which are abundantly represented in contemporary Globigerina Ooze, but have not been found in deposits older than Quaternary, and the Zygosphaeraceae which are not represented in bottom deposits at all.

Coccolithus pelagicus (Wallich) Schiller

Plate 143, figs. 1, 2

This is the most familiar of all coccoliths; it was discovered in samples of ooze raised from the floor of the North Atlantic Ocean during the first telegraph surveys, and was examined by Huxley and Wallich, and later by Murray and Blackman (1898). The living

EXPLANATION OF PLATE 143

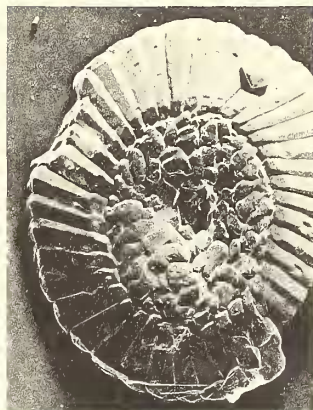
- Figs. 1, 2. *Coccolithus pelagicus* (Wallich) Schiller, recent Globigerina Ooze, *Discovery II* Sta. 4269, Biscay Abyssal Plain. 1, No. 20175, oblique distal view, $\times 4800$. 2, No. 5000, details of central area, distal view, $\times 5000$.
- Fig. 3. *Coccolithus* sp. cf. *C. cavus* Hay and Mohler; No. 22279, Upper Oligocene, core DWBG 10, Pacific Ocean; distal view, $\times 5300$.
- Fig. 4. *Coccolithus* sp. cf. *C. marismontium* Black; No. 22284, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view, $\times 6700$.
- Figs. 5, 6. *Ellipsagelosphaera* sp. 5, No. 15230, Campanian Chalk, Belgorod, Russia; distal view, $\times 8000$. 6, No. 22874, Cambridge Greensand, Cherry Hinton Fields, near Cambridge; complete coccosphere (calcified cyst), $\times 3700$.



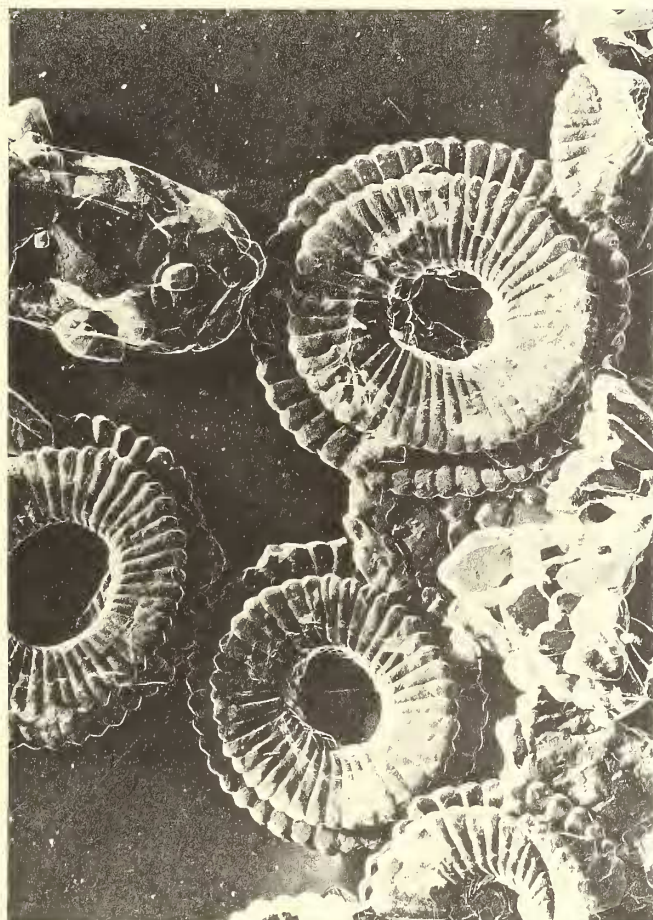
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alga is confined to the North Atlantic, and is the only species that is known to have a preference for cold water; all attempts to find it in Antarctic waters of suitable temperature have failed. This was apparently not the case during the Pleistocene, for Allan Bé and his colleagues at the Lamont Observatory have found it in core-samples from the southern oceans at levels dated as belonging to the middle of the Wisconsin glacial episode (McIntyre and Bé 1967). In the Tertiary, there are very similar forms, but studies under the electron microscope show that they are specifically distinct (Pl. 143, fig. 3). The same generic form can be traced back to the Eocene, but once we pass into the Mesozoic, the species that superficially resemble *C. pelagicus* are obviously different in the finer details of their construction. When the coccoliths are examined under a petrological microscope, with the fossil lying flat on the slide, Tertiary and living species give an interference figure in which the distal shield plays no part, since the optic axes of the component calcite crystals are at right-angles to the plane of the shield. In the Mesozoic genus *Ellipsagelosphaera* this is not the case, and the crystals of the distal shield show strong birefringence, so that the optical figure takes a complicated form, due to the superposition of two black crosses, one produced by each shield. In addition, the Mesozoic species always have a corona of quadrate or keystone-shaped crystals lying on top of the distal shield, and marking off the central area (Pl. 143, fig. 5). Under an ordinary microscope the Tertiary and Mesozoic species look very much alike, but under a polarizing microscope or an electron microscope they are so obviously distinct that they are now placed in separate subfamilies.

In the Jurassic and Cretaceous there are also several other genera such as *Sollasites* (Pl. 144, figs. 1, 2), which resemble *Coccolithus* in a general way, but differ considerably in the finer details of their structure. They are clearly not on the main line of descent towards the *C. pelagicus* stock, but some of them may prove to be ancestral to certain other Tertiary and living forms.

Cyclococcolithus leptoporus (Murray and Blackman) Kamptner

Plate 144, figs. 3, 4; Plate 147, fig. 1

On theoretical grounds, Kamptner has argued that the circular outline is more primitive than the elliptical, and has insisted upon the taxonomic separation of these two shapes (compare Pl. 143, figs. 1–6, Pl. 144, figs. 3–7). He remarks:

‘Above all else, one clear-cut taxonomic principle is decisive for subdivision . . . into tribes and subtribes: a sharper separation of the circular from the elliptical forms. A primitive character must be attributed to the circular outline, and a derivative character to the elliptical. . . . It is also *a priori* conceivable that the change-over from the circular to elliptical types has been achieved polyphyletically, and so to speak on a broad front’ (Kamptner 1958, p. 64).

In accordance with this principle, he removed *Coccolithus leptoporus* to a new genus, *Cyclococcolithus*, and similarly split up other genera so that species with circular coccoliths could be put into different subtribes from those with elliptical coccoliths.

Cyclococcolithus leptoporus provides a convenient starting point from which to examine this taxonomic principle in relation to the geological record. This species is abundant in the living plankton, and is widely distributed. Very similar coccoliths are common in the Pliocene, and particularly so in core-samples from the ocean floor (Pl. 144, fig. 4).

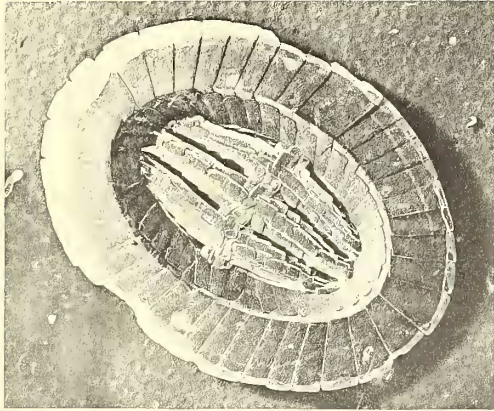
In such deposits, the two discs of the placolith are apt to become separated, and many records of *Tiarolithus* and *Calcidiscus* from the Upper Tertiary are probably based upon dismembered specimens of *C. leptoporus* or closely related species. Other species are found in the Lower Tertiary, and the earliest record of the genus is from the Danian. These early forms occur associated with characteristically elliptical species of *Coccolithus*, and the two stocks were quite distinct from each other at the time of their first appearance in the early Tertiary. Thus the Tertiary record does not give much support to the idea that the circular shape is primitive; indeed, it tends to emphasize the complete independence of the elliptical forms rather than to provide any suggestion of their descent from circular ancestors.

This independent relationship is emphasized by a curiously similar state of affairs in the Upper Jurassic, for a different set of circular and elliptical types exist side by side in the Oxford and Kimeridge Clays. These include the genera *Cyclagelosphaera* and *Ellipsagelosphaera* (Noël 1965), which at first sight appear to be so much like *C. leptoporus* and *C. pelagicus* that they were originally recorded under these names. This resemblance, however, is illusory, for there are significant differences in micro-structure. It is remarkable that the two Jurassic genera each differ from their Tertiary analogues in exactly the same way: they both have strongly birefringent distal shields, surmounted by a well-developed corona (compare Pl. 143, fig. 3 and Pl. 144, fig. 3 with Pl. 143, fig. 5 and Pl. 144, fig. 5). Consequently, if we focus our attention on the minutiae of crystal-arrangement, we find that the Jurassic circular forms resemble their elliptical contemporaries more closely than they resemble modern circular forms. Are we then to unite the Jurassic genera, both circular and elliptical, into one family or subfamily, as Noël (1965) has done, or would it be more reasonable to keep the two shapes separate, regarding them as two parallel stocks that became independent at an early stage, and have remained so ever since?

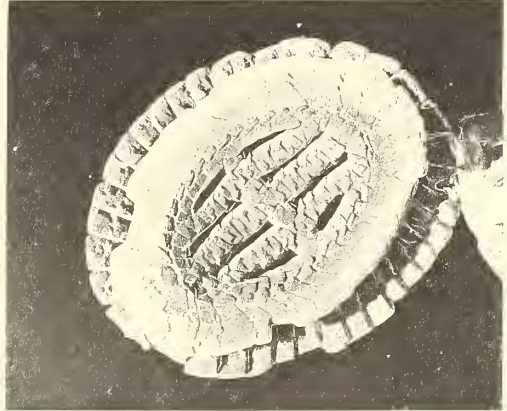
An attempt to answer this question requires a closer look at the geological history of these two stocks. The elliptical forms are abundant throughout the Mesozoic and Cainozoic, and it may be that within this multitude of species there exists a continuous evolutionary thread leading from the Jurassic to the present day. The only serious break in this record is at the Cretaceous-Paleocene boundary, and there is not enough information available at present to reach a decision. The history of the circular placoliths is rather different. After the great abundance of *Cyclagelosphaera* (Pl. 144, fig. 5) in the Jurassic, there is a paucity of circular forms in the Cretaceous. The few examples that

EXPLANATION OF PLATE 144

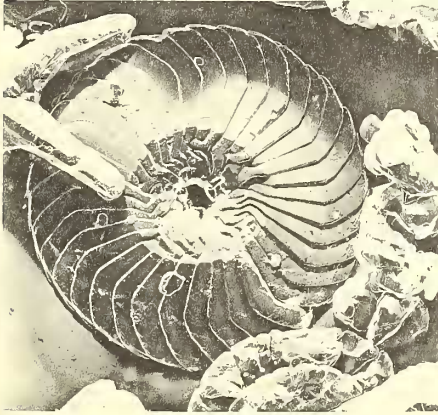
- Figs. 1, 2. *Sollasites horticus* (Stradner *et al.*) comb. nov. (= *Coccolithus horticus* Stradner *et al.*), Cambridge Greensand near Cambridge, $\times 9600$. 1, No. 4706, Barrington, distal view. 2, No. 21739, Cherry Hinton Fields, proximal view.
- Figs. 3, 4. *Cyclococcolithus* spp., Lower Pliocene, core LSDH 78P, Pacific Ocean. 3, cf. *C. leptoporus* (Murray and Blackman) Kamptner, No. 22224, distal view, $\times 4000$. 4, No. 22210, group with some specimens in the 'Calcidiscus' condition, $\times 2500$.
- Fig. 5. *Cyclagelosphaera margereli* Noël; No. 17410, Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole; distal view, $\times 10\ 000$.
- Fig. 6. *Markalius* sp. cf. *M. inversus* (Deflandre) Bramlette and Martini; No. 17199, Belemnite Marl (L. Turonian), Cherry Hinton, near Cambridge; proximal view, $\times 6000$.
- Fig. 7. *Ericsonia* sp.; No. 22295, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view, $\times 6000$.



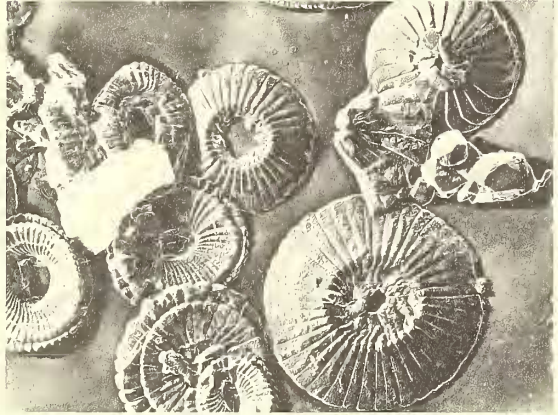
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are known, such as *Markalius* (Pl. 144, fig. 6), can hardly be regarded as linking *Cyclagelosphaera* with *Cyclococcolithus*, because they have a more complicated structure than either of these. They seem rather to be leading towards *Ericsonia* (Pl. 144, fig. 7) and other still more specialized forms that flourished in the Lower Tertiary. There is thus a gap extending throughout the Cretaceous period, during which they were apparently no representatives of the hypothetical *Cyclococcolithus* lineage. It seems, therefore, unlikely that the Tertiary species originated as an offshoot from *Cyclagelosphaera*, and it is more probable that they developed from an unknown ancestor early in the Tertiary.

The evidence from the geological record thus seems to alienate the Mesozoic circular forms from their modern analogues, and the evidence of morphology throws them into association with their elliptical contemporaries, in spite of the difference of shape.

Coccolithus huxleyi (Lohmann) Kamptner
(= *Emiliania huxleyi* (Lohm.) Hay and Mohler 1967)

Plate 145, figs. 1, 2

The taxonomic position of this species is surrounded by interesting problems. It stands apart from *C. pelagicus* and all other living members of the genus in the peculiar construction of its shields, and its conspicuous central grid, which recalls the similar structures in many extinct forms. Mary Parke in Parke and Dixon (1964, p. 520) has pointed out that the motile phase lacks an obvious haptonema, and in this respect it resembles the Isochrysidales rather than the Coccolithophorales. Paasche (1964, p. 11) found in his cultures that coccolith-secreting individuals were without visible flagella, although these could be seen on some of the naked cells.

In the living plankton, it is undoubtedly the most vigorous and successful of the coccolith-bearing algae. It is distributed over the whole area of the oceans from the Antarctic convergence to the Arctic, and can invade brackish waters inaccessible to other pelagic species. Because of its great vigour and tolerance, it has provided material for more laboratory experiments than any other species.

C. huxleyi is apparently a very recent addition to the oceanic plankton. McIntyre and Bé (1967) have reported its first appearance in deep-sea cores as taking place within Brunhes Normal Zone (that is, less than 700 000 years ago, and more probably nearer to 100 000 years). They also report the presence of a coccolith intermediate between *C. huxleyi* and *Gephyrocapsa oceanica* in cores spanning the interval between 300 000 and 100 000 years. *G. oceanica* (Pl. 145, fig. 3) can be traced back into the Pliocene, and survives in the living plankton. Forms with the oblique bridge characteristic of *Gephyrocapsa* are unknown before the Pliocene, but the other characters of the genus, such as the large central opening with a bilateral grid, and the non-imbricate ray-elements, are strongly developed in a host of Lower Tertiary species of *Tremalithus* (Pl. 145, figs. 4–6). There is a great diversity of species with elaborate grids in the Middle and Upper Eocene, and the same type of coccolith can be traced back still further into the Mesozoic. The earliest representatives, with rather simpler grids, are found in the Lower Gault (Middle Albian) at Folkestone (Pl. 145, figs. 7, 8).

The taxonomic isolation of *C. huxleyi* from the rest of the genus *Coccolithus*, which is suspected from the peculiarities of the living alga, is thus confirmed by its long and independent geological history, and there can be little doubt that this species should be

removed to a separate genus, and possibly to a family independent of the Coccolithophoraceae.¹

Pontosphaera discopora Schiller

Plate 146, figs. 1, 2

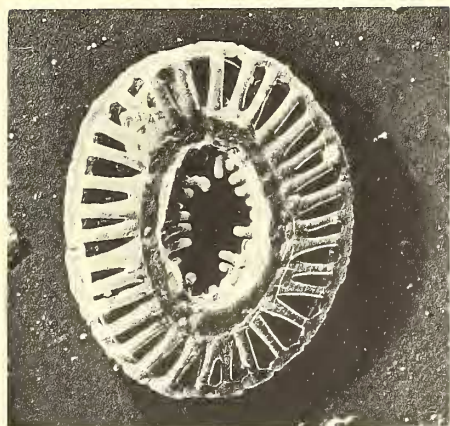
The genus *Pontosphaera* was created by Lohmann (1902) for species in which the coccoliths appear to be simple discs, with or without a shallow rim. The outline is elliptical, and the coccoliths are most commonly shaped like a shallow pie-dish. Specific diagnoses were originally based upon work under the biological microscope, and later studies in polarized light or under the electron microscope have led to the removal of several species to other genera. No electron micrographs of the type species, *P. syracusana*, have yet been published, but Mrs. Gaarder has generously allowed me to compare some of her excellent micrographs of this species with my Tertiary material. The coccoliths are large, with a floor perforated by about 750 very delicate pores, and the wall is constructed of about 200 very slender and steeply inclined calcite laths. *P. discopora* has similarly constructed but smaller coccoliths, with larger and less numerous pores. The Tertiary coccoliths discussed below have the same general type of structure, and can with reasonable confidence be referred to the same genus as *P. syracusana* and *P. discopora*.

Coccoliths of various species of *Pontosphaera* are not uncommon in modern Globigerina Ooze, particularly beneath the warmer parts of the oceans. In the Pliocene a form closely resembling *P. discopora* is occasionally found (Pl. 146, figs. 4, 5), but other species are rare or absent, and none of the modern perforated species has yet been identified with certainty in pre-Pliocene sediments. Nevertheless, coccoliths with all the characteristic features of *Pontosphaera* except the circular pores in the floor, are widely distributed throughout the Tertiary. There appear to be several lineages among these Tertiary species, each with a slightly different pattern in the structure of the floor. One of these is of special interest, since it appears to connect the living *P. discopora* with a complex of Eocene forms whose ancestry can probably be traced back to the Cretaceous. The proximal surface of the floor in this series has a bilateral arrangement of plates similar to that originally described by Kamptner in *P. scutellum*, and now known in a number of diverse Eocene forms (Pl. 146, fig. 6). The distal side has an entirely different

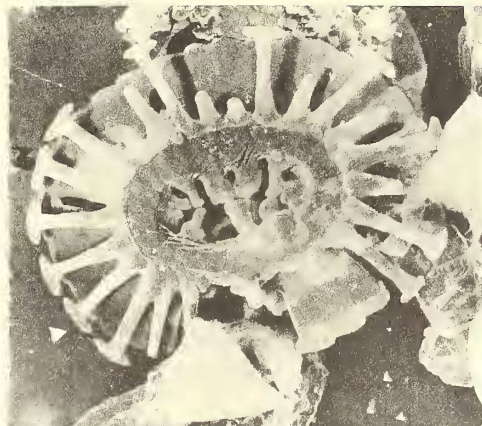
EXPLANATION OF PLATE 145

- Figs. 1, 2. *Coccolithus huxleyi* (Lohmann) Kamptner; recent oceanic deposits. 1, warm-water form, No. 3421, *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 16\ 000$. 2, cold-water form, No. 11612, *Discovery II* Sta. 3809, Galicia Bank; distal view, $\times 20\ 000$.
- Fig. 3. *Gephyrocapsa oceanica* Kamptner; No. 18072, modern Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts., proximal view, $\times 8000$.
- Figs. 4-8. *Tremalithus* spp. 4, *T. danicus* (Black) comb. nov. (= *Dictyococcites danicus* Black); No. 11819, Middle Oligocene, Grundf r, Denmark; proximal view, $\times 6000$. 5, *T. placomorphus* Kamptner; No. 22838, Lower Oligocene, Rodstenseje nr. Odder, Denmark; proximal view, $\times 4000$. 6, *T. dictyodus* (Deflandre and Fert) comb. nov. (= *Discolithus dictyodus* D. and F.); No. 22831, Lower Oligocene, Rodstenseje nr. Odder, Denmark (possibly reworked from M. Eocene); proximal view, $\times 6100$. 7, *T. burwellensis* Black; No. 14622, Cambridge Greensand (Cenomanian), Barrington near Cambridge; distal view with proximal shield showing through, $\times 10\ 000$. 8, *T.* sp., No. 13371, Lower Gault (M. Albian), Folkestone, Kent; proximal view, $\times 8000$.

¹ Since this lecture was delivered, a paper by W. W. Hay *et al* has been received, in which *C. huxleyi* has been formally transferred to a new genus, *Emiliania*.



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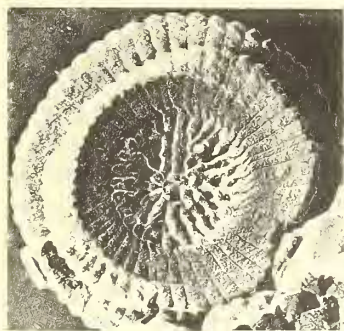
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appearance, with a pattern of concentrically arranged fibrous elements (Pl. 146, figs. 3, 7). This combination of patterns is also seen in several species of *Helicosphaera* (Pl. 147, figs. 1-3), and will be considered further in connection with the ancestry of that genus.

This constructional pattern can be picked up again in the late Cretaceous. Two species in the Santonian and Campanian have the same kind of wall-structure, and the same arrangement of plates on the proximal surface. One of these, *Pontolithina moorevilensis*, has two small perforations at the foci of the ellipse (Pl. 149, fig. 4). This species may well prove to be the ancestor of several Tertiary lineages. Obliteration of the two pores and an increase in the number of wall-elements would give a form very much like certain Eocene species, for example *P. versa* Bramlette and Sullivan (Pl. 146, fig. 6), *P. vadosa* Hay *et al.*, and possibly other forms like *Discolithus oamaruensis* Defl. Enlargement of the pores to make two circular windows would lead to such forms as *D. duocavus* Bram. and Sull. (L. Eocene) and *D. panarium* Defl. (M. Eocene).

There are also several Eocene species which differ in having numerous small circular pores, but which probably have a comparable floor-structure, since they give similar interference patterns in polarized light; their ultra-structure has not yet been examined under the electron microscope. *D. punctosus* Bram. and Sull. (L. Eocene) and *D. distinctus* Bram. and Sull. (M. Eocene) have this structure; they foreshadow the modern perforate species of *Pontosphaera*, but in the absence of any recognizable intermediates in the Upper Eocene and Miocene, we cannot say whether there is any direct phylogenetic connection. Possibly *D. vigintiforatus*, the type species of *Discolithus* from the Miocene of the Vienna basin, may yet prove to be on this line of descent.

There can be little doubt that *Pontosphaera* has a long geological history, and that many Tertiary species that have been referred to the rather unsatisfactory form-genus *Discolithus* actually fit quite naturally into one or other of the lineages of this complex. A derivation from some branch of the Mesozoic Zycolithaceae seems quite possible, and is indeed suggested by the presence in the Upper Cretaceous of forms that are intermediate between the two families (Pl. 149, fig. 4).

Helicosphaera carteri (Wallich) Kamptner
(= *Helicopontosphaera kamptneri* Hay and Mohler 1967)

Plate 147, figs. 1, 2

In the present-day oceans, the genus *Helicosphaera* is represented by a single species whose coccoliths are peculiar in having a spiral brim which terminates in a characteristically flaring wing. Within this brim is an elliptical shield, shaped rather like the crown of a hat; it has bilaterally arranged plates on the proximal side, and concentric fibres on the distal, so that the structure is much the same as in many species of *Pontosphaera*.

This species has been customarily regarded as closely related to, and possibly derived from taxa such as *Coccolithus* with typical placoliths. Study of *H. carteri* under the electron microscope does not give much support to this idea; the coccoliths are clearly not mis-shapen placoliths, as is often assumed, and it is difficult to see how the spiral flange could have been derived from the two shields of a placolith. Compared with other living coccolithophorids, *H. carteri* stands very much by itself, and its geological history abundantly confirms its independence from the Coccolithophoraceae.

At the present day *H. carteri* is confined to the parts of the oceans lying roughly between latitudes 50° N. and S.; in bottom sediments its range is withdrawn a little towards the equator (McIntyre and Bé 1967, p. 585). In the Pliocene, forms that would be difficult to separate from this species are widely distributed, both in deep-sea cores and in samples collected on land. Similar forms, still very much like *H. carteri*, are abundant in the Upper Miocene, but here they are associated with several extinct species which are obviously quite different. In the underlying parts of the Miocene and in the Oligocene and Eocene there is a varied complex of extinct species, and the genus was evidently undergoing a burst of evolutionary diversification, possibly at its climax during the Oligocene.

In the early Eocene there are several species whose coccoliths lack the broad, flaring wing that is so characteristic of later species; they have a shape that does not depart much from an ovoid or even a regular ellipse. The earliest of these, *H. semiuulium*, evolves from a Lower Eocene population in which this simple type (subspecies *seminulum*) is predominant (Pl. 147, fig. 4), to a Middle Eocene population in which the predominant subspecies *lophotus* is much more like a typical *Helicosphaera* (Bramlette and Sullivan 1961). The rim in subsp. *seminulum* shows little more than a suggestion of spiral structure, and in fact resembles the wall of an early Tertiary *Pontosphaera* crossed by an oblique wrinkle. The resemblance between these primitive species of *Helicosphaera* and some of the contemporary species of *Pontosphaera* is so close that they might reasonably be placed in the same genus, were it not that forms like *H. semiuulium* are so plainly ancestral to other more typical species of *Helicosphaera*.

We have thus traced the ancestry of *H. carteri* back to an early stage when the genus was barely distinguishable from *Pontosphaera*, and we are now in a better position to assess its taxonomic status. It clearly has no close relationship with the Coccolithophoraceae, and must be placed in some other family. It has sprung from the same ancestors as the living *Pontosphaera*, and for this reason might be included in the Pontosphaeraceae. On the other hand, it can be argued that the divergence between the two stocks since the early Tertiary has been so profound that the living representatives can hardly be included in a single family, and I have proposed elsewhere that a new family, the *Helicosphaeraceae*, should be established for *H. carteri* and the numerous Tertiary species of which it is the sole survivor (Black 1968).

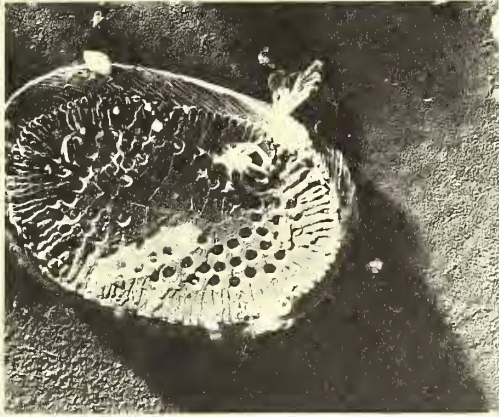
Braarudosphaera bigelowi (Gran and Braarud) Deflandre

Plate 147, fig. 5

In 1935 a new species, thought to be a *Pontosphaera*, was recorded in plankton hauls from the Bay of Fundy (Gran and Braarud 1935); this was re-examined by Deflandre,

EXPLANATION OF PLATE 146

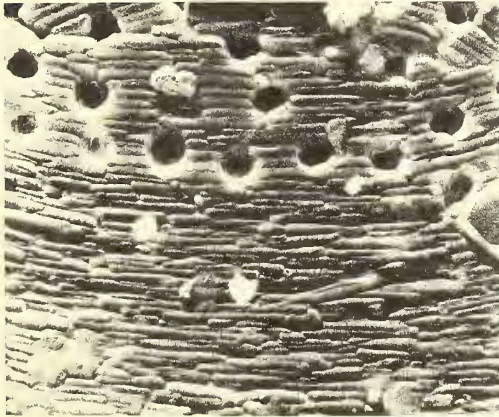
Figs. 1-7. *Pontosphaera* spp. 1-3, *P.* sp. cf. *P. discopora* Schiller, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean. 1, No. 11393, proximal view, $\times 7200$. 2, No. 11318, distal view, $\times 8000$. 3, No. 11319, details of distal surface, $\times 24\ 000$. 4, 5, *P.* sp. cf. *P. discopora* Schiller, Pliocene, Cisano nr. Albenga, Italy. 4, No. 16852, proximal view, $\times 4800$. 5, No. 16854, oblique proximal view, $\times 4000$. 6, 7, *P. versa* (Bramlette and Sullivan) comb. nov. (= *Discolithus versus* B. and S.), Eocene, Tuilerie de Donzacq, Landes, France. 6, No. 15855, proximal view, $\times 6000$. 7, No. 15834, distal view, $\times 6000$.



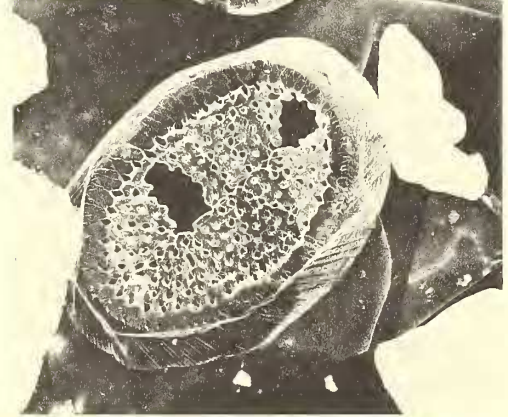
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who showed that its coccoliths were entirely different from any previously known form. They consist of five peculiarly shaped calcite plates arranged to form a regular pentagon, and twelve of these pentoliths fit together to make a dodecahedral skeleton enclosing an encysted cell. The species was re-named *Braarudosphaera bigelowi*, and a new family was based upon it (Deflandre 1947). At that time little was known about its geological history, which we now know to be quite remarkable. Coccoliths with exactly the same structure have been found at various levels in the Tertiary, and are abundant in the Upper Bracklesham Beds of the Sussex coast. They have also been found, though less abundantly, throughout the Cretaceous system, and except for an increase in size in the older specimens, are specifically indistinguishable from recent material. No other species of coccolithophorid has a stratigraphical range at all comparable with this, and at first sight it might be thought that we have here an extreme example of specific stability. This is no doubt true of the main lineage of *B. bigelowi* itself, but in the Tertiary we are confronted not only with a multiplicity of other species of *Braarudosphaera* itself, but in addition an exuberant development of two closely related genera, *Micrantholithus* and *Pemna* (Pl. 147, fig. 6), all with coccoliths constructed on the same pentolith system. Detailed phylogenies have still to be worked out, but some of the simpler forms are so close to *B. bigelowi* that there can be little doubt about their origin.

B. bigelowi is an unquestionable example of a single living species that is the sole survivor of an important and diversified Tertiary family whose ancestry can be traced back well into the Mesozoic. This point is stressed because there are several other species in the living plankton with very much the same kind of history, resulting in a taxonomic isolation which is equally real, but by no means always so obvious.

CALCIOSOLENIACEAE Kamptner

Plate 148, figs. 1, 2

Most coccolithophorids have a spherical, egg-shaped, or pear-shaped body. The Calciosoleniaceae differ in being cylindrical or fusiform, and their coccoliths instead of being circular or elliptical, take the form of a narrow parallelogram (Pl. 148, fig. 1). There are probably four or five living species, and although the family characters are unmistakable, their systematics at generic and specific levels are not easy. Fossil representatives are never common, but have been found at intervals in the geological column down to the Cretaceous, the earliest British occurrence being at the base of the Cenomanian (Pl. 148, fig. 2); Stradner (in Stradner *et al* 1968) has recently announced the discovery of similar specimens in the Albian of Holland. The interesting feature of this record is that the earliest specimens differ so little from living material: the family characters with all their eccentricities are fully developed at the first appearance, there is no clue at all about relationships to other coccolith taxa, and no suggestion of any evolutionary change during the long interval from the middle Cretaceous to the present day.

LIVING FAMILIES WITH NO KNOWN GEOLOGICAL RECORD

We have now considered a number of isolated species in the living plankton, many of which have turned out to be survivors of once flourishing families that are otherwise

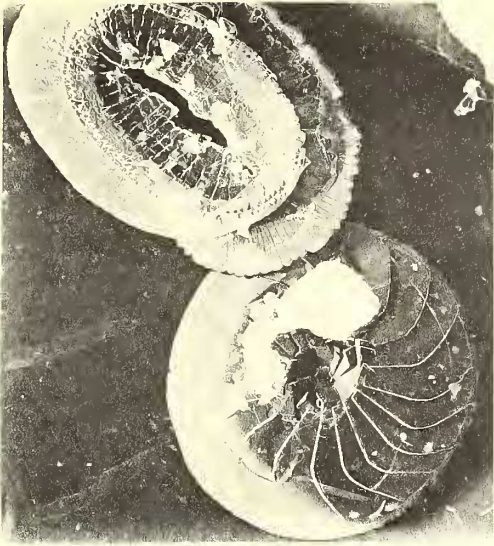
extinct. In contrast with these are the two largest living families, the Syracosphaeraceae and Zygosphaeraceae, which have no fossil record behind them. Both families have more than 50 species, and together they account for more than half the living coccolithophorids. The Zygosphaeraceae are all holococcoliths: that is, they are constructed of minute rhombohedra or prisms of calcite, each enclosed in an organic membrane. Such structures are very delicate, and would probably break down into their component crystals soon after falling to the sea floor; this may well be the reason why they are not found in the Globigerina Ooze or other oceanic deposits. This, however, can hardly be true of the Syracosphaeraceae, which are much more robustly constructed. Many species of *Syracosphaera* are, indeed, found abundantly in the modern Globigerina Ooze, and their absence from the Pliocene and older deposits therefore calls for some different explanation. (W. W. Hay and his colleagues have recently referred two Tertiary species to this genus (*S. bisecta* Hay *et al.* 1966, p. 393, and *S. clathrata*, 1967, p. 449). *S. bisecta* has been re-examined by Bramlette and Wilcoxon (1967, p. 102), who regard it as a species of *Coccolithus*, and until more is known about the wall-structure of *S. clathrata*, its reference to *Syracosphaera* cannot be regarded as fully established.) The obvious conclusion that the Syracosphaeraceae are, in fact, post-Tertiary additions to the oceanic plankton is probably correct, and will be considered later in relation to the abrupt appearance of other cryptogenic families in earlier times.

EXPLANATION OF PLATE 147

- Figs. 1-4. *Helicosphaera* spp. 1, 2, *H. carteri* (Wallich) Kamptner, recent Globigerina Ooze. 1, No. 18030, *Discovery II* Sta. 4288, Biscay Mts., proximal view, $\times 7200$. Also *Cyclococcolithus leptoporus* (M. and B.) Kamptner, distal view. 2, No. 13137 from *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 7200$. 3, *H.* sp., No. 22839, Lower Oligocene, Rodtenseje nr. Odder, Denmark; proximal view, $\times 3200$. 4, *H. seminulum* Bramlette and Sullivan; No. 14293, Middle Eocene, core DWBG 23B, Pacific Ocean; proximal view, $\times 6700$.
- Figs. 5, 7. *Braarudosphaera* spp. 5, *B. bigelowi* (Gran and Braarud) Deflandre; No. 15730, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; complete coccolith of five plates, $\times 4000$. 7, *B. africana* Stradner; No. 16057, Sutterby Marl (Aptian), borehole Alford, Lincs., 101-7 ft.; complete coccolith, $\times 4000$.
- Fig. 6. *Penma papillatum* Martini; No. 15871, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; single plate, $\times 5000$.

EXPLANATION OF PLATE 148

- Fig. 1. *Calciosolenia* sp., No. 13131, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; proximal view, $\times 10\ 000$.
- Fig. 2. *Scapholithus* sp., No. 20678, Chalk Marl, (Cenomanian), Folkestone, Kent; proximal view, $\times 13\ 000$.
- Figs. 3, 4. *Syracosphaera* spp. 3, *S. hystrica* Kamptner; No. 2573, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 16\ 000$. 4, *S. pulchra* Lohmann; No. 18062, recent Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts.; proximal view, $\times 6000$.
- Fig. 5. *Loxolithus armilla* (Black) Noël, holotype, No. 2807, Burwell Rock (Cenomanian), Great Shelford nr. Cambridge; distal view, $\times 8000$.
- Figs. 6, 9. *Rhabdolithina* spp. 6, *R.* sp., No. 18616, Sutterby Marl (Aptian), borehole, Alford, Lincs., 101-7 ft.; oblique proximal view, $\times 6000$. 9, *R.* sp., No. 13501, Lower Gault (Albian), Folkestone, Kent; oblique proximal view, $\times 8000$.
- Fig. 7. *Stanrolithites* sp., No. 21747, Cambridge Greensand (Cenomanian), Cherry Hinton Fields nr. Cambridge; distal view, $\times 8000$.
- Fig. 8. *Zygodolithus diplogrammus* Deflandre; No. 22337, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; distal view, $\times 5300$.



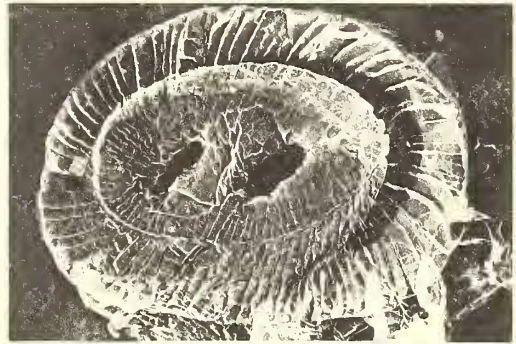
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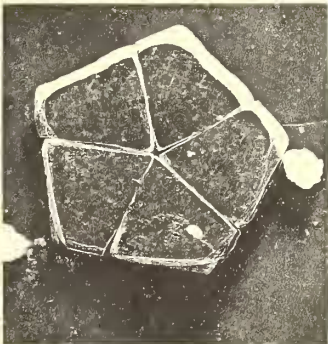
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